SENSORY SPINES IN THE JURASSIC
BRACHIOPOD *ACANTHOTHIRIS*

by M. J. S. RUDWICK

ABSTRACT. The rhynchonelloid *Acanthothiris* has tubular external spines similar to the spines of productoids and chonetoids. Their structure, arrangement and mode of growth are described in detail, on the basis of a study of exceptionally well-preserved specimens of *A. spinosa*. They are compared to the spines of the related genus *Acanthorhynchia*, and to those of the living oyster *Crassostrea echinata*. On the basis of the known sensory physiology of living brachiopods, it is inferred that the spines near the valve-edges of *Acanthothiris* contained extensions of the mantle, and that their tips bore portions of the highly sensitive mantle-edge tissue. These sensitive spine-tips could have provided the brachiopod with effective 'early warning' protection against potentially harmful agents in the environment; and the radiating spines themselves could have formed a protective grille straddling the apertures leading into the mantle cavity. Spines further from the valve-edge are blocked, and are regarded as having been superseded functionally. This interpretation is discussed in relation to the spines of other brachiopods and *Crassostrea*, and in relation to the ontogeny, ecology and phylogeny of *Acanthothiris*.

TUBULAR external spines were developed in great abundance and diversity in one sub-order of the Brachiopoda, namely the Upper Palaeozoic Productoidea. Similar spines, developed only in one particular position on the shell, characterize another Upper Palaeozoic suborder, the Chonetoidea. Outside these two suborders, tubular spines are rare and sporadic. This paper is concerned with one of the best known of these anomalous genera, the Jurassic rhynchonelloid *Acanthothiris*. This is separated by a span of about 100 million years from the last of the spiny productoids and chonetoids, and is even more decisively separated from them by morphology and taxonomy. In all characters except the spines, it is a 'normal' rhynchonelloid. It thus illustrates a common phenomenon in brachiopod evolution: a structure characteristic of some major group is often found to have been evolved independently by one or a few anomalous genera which clearly belong (on every other criterion) to a quite different group (cf. Williams 1956). A functional analysis of the spines of *Acanthothiris* may help to throw light on this phenomenon.

Material. For this study, I have used a small collection of very well-preserved specimens of *A. spinosa* (Schlotheim), the genotype, from the Inferior Oolite (Middle Jurassic) of 'Collier's Lane, nr. Bath' (Sedgwick Museum, Cambridge, SM J57751–71), together with some similar specimens from another old collection, labelled 'Gt. Oolite, Bath' (Museum of Comparative Zoology, Harvard, MCZ 5794). Despite the difference of labelling, all these specimens may come from the same locality. 'Collier's Lane' is un-fortunately not mentioned by name in Richardson's (1907) account of the stratigraphy of the Inferior Oolite around Bath. Richardson records *A. spinosa* from most units of the Inferior Oolite; but the matrix suggests that the specimens came from the Upper Trigonia Grit. The matrix is a hard oolitic limestone, but it has weathered in pockets to a much softer material which, with care, can be dissected away from the spines. Normally only the stumps of the spines are preserved.

For comparative purposes, I have also studied the closely related species *Acantho-*

rhynchia senticosa (von Buch) from the Inferior Oolite of Dorset. There are no living brachiopods with true tubular spines. But the mollusc *Crassostrea echinata* (Quoy and Gaimard) is a possible functional analogue. I have collected this oyster from intertidal localities on the Queensland coast and offshore islands, and studied it alive in a small aquarium.

The photographs in this paper were taken with a Leitz Aristophot on Ilford Pan F film; all except Plate 86, fig. 5 were lightly coated with ammonium chloride.

STRUCTURAL ANALYSIS

General description. The shells of *Acanthothiris* (the 'corrected' spelling *Acanthothyris* is invalid: see Ager 1960) are typically 'rhynchonelloid' in form. They are strongly biconvex in profile, broadly elliptical in plan, and have a non-strophic hinge. There is a small incurved ventral umbo; the dorsal umbo is tucked inside the delthyrium. There is a dorsal median deflexion in the commissure, a low median fold on the dorsal valve, and a shallow median sulcus on the ventral. The surface of each valve is covered with a pattern of fine costellae radiating from the umbo. On most specimens, the costellae appear to be swollen at intervals into small pustules (Pl. 84, fig. 1); but well-preserved specimens show that these pustules are in fact the broken stumps of slender spines.

The whole *array* of spines covers almost all parts of the valve-surfaces. The spines are arranged in *rows* corresponding to the costellae from which they project, radiating from the umbo of each valve towards the valve-edge. The number of rows, like the number of costellae, increases progressively in this direction. Within each row, the spines project from the costella at fairly regular intervals (Pl. 84, figs. 1–3; Pl. 85, figs. 1, 3, 4). They are not arranged regularly in concentric fashion, but it will be convenient to refer to a *set* of spines as those projecting from any narrow concentric zone of the valve-surface (cf. Rudwick 1959). On most parts of the shell the spines project almost tangentially from the curved surface of the valves; but in the lateral sectors, and especially near the commissure, they project at higher angles and even perpendicularly (Pl. 84, fig. 5).

The spines are very rarely preserved to their full length; some have been dissected from the matrix to a length of 8 mm. (Pl. 85, fig. 5) but were certainly longer than this. They are cylindrical; at the base they are about 0·5 mm. in diameter, but they taper gradually to about 0·2 mm. diameter on those preserved to the greatest length (Pl. 84, fig. 6; Pl. 85, figs. 1, 5; Pl. 86, figs. 1, 5). They are straight or slightly curved. They are composed of an external sheath of dense primary-layer shell, of matt appearance, within which there is generally an almost solid core of shiny fibrous secondary-layer shell. The contrast between the two layers is easily seen at the broken tips of the spines (Pl. 86, fig. 5) or on the broken stumps (Pl. 85, fig. 2).

Mode of growth of spines. Since the spines are sheathed in primary-layer shell, which is continuous with that of the rest of the valve, it is clear that they are derivatives of the valve-edge, at which the primary-layer was secreted. Their mode of growth can be

reconstructed from a study of individual spines preserved at various stages of growth, and from the growth-lines on the primary-layer.

The commissure was affected throughout ontogeny by a serial deflexion of small wavelength and low amplitude. Thus the valve-edges were slightly crinkled and interlocked with one another (Pl. 84, fig. 2; Pl. 86, figs. 6, 7), while the cumulative effect of the deflexion was to produce the costellae on the valve surfaces. Each spine first appeared at the valve-edge on one of the crests (text-fig. 1A) of the deflexion. Initially it was marked only by a slight expansion of the valve-edge at this point (text-fig. 1B). Successive increments of primary-layer accentuated this into a small 'collar' (text-fig. 1C). At the next stage observed the 'collar' had been completed into a shelly ring surrounding a small foramen, while the main growing-edge had resumed its normal form (text-fig. 1D). In other words, a small circle of valve-edge had, in effect, been 'budded off' from the
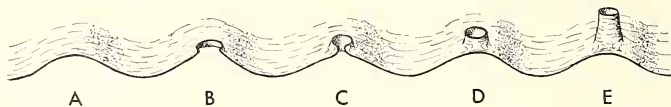
TEXT-FIG. 1. Initial stages in the growth of a tubular spine at a valve-edge in *Acanthothiris*. For further explanation, see text. Semi-diagrammatic, about × 20.

rest of the valve-edge. Thereafter it grew independently, adding circular increments of primary-layer, which lengthened the ring into a tube; while the continued growth on the main growing-edge isolated the base of the incipient spine further from the valve-edge (text-fig. 1E). All these early stages in the growth of a spine can be recognized near the valve-edges of well-preserved specimens (Pl. 84, figs. 3, 4; Pl. 86, figs. 2, 3, 4). Further growth at the distal end of the spine, with a gradual reduction in the diameter of the circle of growing-edge, would have produced the long, gently tapering form of the full-grown spines.

Relation of spines to mantle-tissue. These growth-stages can be interpreted in terms of the secretory activity of the mantle-tissue by using the standard homological relation between shell and mantle as known in living brachiopods (cf. Williams 1956). Thus the budding-off of a ring of valve-edge material reflects an identical budding-off of a ring of mantle-edge tissue, by which the primary-layer was secreted. Each hollow-growing spine must have been lined with an inner tube (or possibly a solid cylinder) of mantle-tissue, connecting the distal ring of mantle-edge tissue to the rest of the mantle. Obviously the spine could have grown in length only so long as this connexion was maintained.

If the spines are examined in cross-section near the base (e.g. where they have all been broken off) it is clear that their walls were progressively thickened with secondary-layer, until the central lumen was constricted to vanishing point. Only the spines nearest the valve-edge (i.e. the youngest spines) have a clear central lumen; those further from the valve-edge (formed earlier in ontogeny) are blocked with concentric layers of shell-material (Pl. 84, fig. 3; Pl. 85, figs. 1, 2; Pl. 86, fig. 4). This secondary-layer material must have been secreted by the inner tube or core of mantle-tissue, which must thereby have been progressively constricted. Ultimately the tissue must have been abandoned; the spine could then have grown no more. The completion of this process is seen also in

the blocking of the internal foramina leading into the spines: these are clearly open near the valve-edges, but are blocked further in from the valve-edges (Pl. 86, figs. 2, 3, 6, 7).

Time-sequence of growth of spines. This distinction between *open* and *blocked* spines leads to an interpretation of the time-relations of the whole array of spines. The spines in each row are those that were successively budded off, during ontogeny, from the same crest of the serial deflexion. The spines in each set, lying on or near any single growth-line on the valve-surface, are those that were formed all round the valve-edge at or about the same time during ontogeny. In any given row, at the moment when a new spine began to be formed at the valve-edge, the immediately preceding spines would still be open, but the earlier ones would have been blocked. On the valve as a whole, at any given moment in ontogeny, the most recently formed set or sets of spines, all round the valve-edge, would still be open, but all those nearer the umbo would have been blocked (Pl. 86, figs. 6, 7). Although a spine might have remained open after ceasing to grow, the converse is of course impossible; hence the actively growing spines must also have been restricted to the peripheral zone of each valve. Each individual spine must therefore have grown relatively quickly to its full length.

Orientation and arrangement of spines. If the shell is described 'statically', the orientation of the spines appears to be rather haphazard: especially in the lateral sectors they seem to project at many different angles (Pl. 84, fig. 2). A more 'dynamic' description, taking into account the time-relations of the spines, reveals a simpler and more orderly arrangement. Seen in plan, each spine projects perpendicularly from the growth-lines on the valve-surface at its base (Pl. 84, fig. 2; Pl. 85, figs. 1–4); in other words, during the time of its formation and growth it projected *radially* from the valve-edge. Seen in profile, each spine projects obliquely from the valve-surface and curves gently towards the opposite valve (Pl. 84, fig. 6; Pl. 86, fig. 1); during the time of its formation and growth it would have projected at a low angle across the plane of the commissure. The most recently formed sets of spines on the two valves would thus have projected radially and interdigitated with each other (text-fig. 2). Since all the spines were formed from the crests of the serial deflexion, and the crests necessarily alternate in position on the two valves, the projecting spines would have alternated likewise, and therefore would not have obstructed the closing of the shell. The spacing of the spines around the valve-edges was markedly uniform at any given growth-stage. In the later stages there was generally a gap of about 0·7 mm. between the bases of adjacent spines. Since the spines diverge and also taper, this spacing would obviously have increased away from the valve-edge.

Ontogeny of spines. The formation of radiating spines began very early in ontogeny. On large shells the stumps of the earliest spines are preserved very close to the umbo of each valve (Pl. 84, fig. 1; Pl. 85, fig. 2). The growth-lines show that they correspond to a stage at which the shell was only about 1·5 mm. broad. A rough estimate from the size of the stumps suggests that the spines themselves were about 0·15 mm. in diameter near the base, and were there separated from each other by spaces about 0·25 mm. across.

During the next stage of ontogeny the diameter and spacing of the spines increased rather rapidly to the adult size (Pl. 84, fig. 2). Thereafter, notwithstanding the progressive increase in the size of the shell, both the diameter and the spacing of the spines remained remarkably constant. This probably reflects a similar constancy in the original length of the spines. The average spacing of the peripheral spines (about 0·7 mm. at the base) was

maintained, in spite of the increasing length of the valve-edges, by the progressive introduction of new rows of spines (borne on new costellae) intercalated between the earlier rows. The effect of this is to be seen in the overall appearance of the whole shell: the bases of the spines appear to be scattered at a uniform density over all parts of the valve-surfaces (Pl. 84, figs. 1–3, 5; Pl. 85, figs. 1–4).
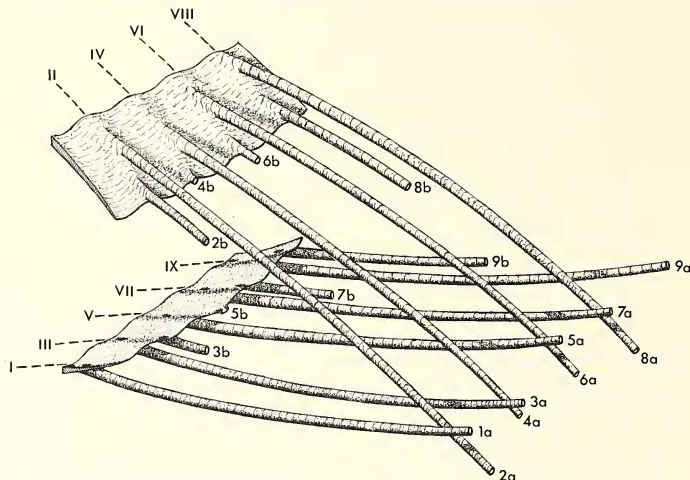
TEXT-FIG. 2. Reconstruction of parts of the valve-edges in *Acanthothiris*, gaping apart as in life, showing grille of spines straddling the aperture, and sensitive spine-tips projecting outwards from the shell; about × 10.

Only the peripheral zone of 'open' spines is shown: note apertures on inner surface of lower valve. Costellae I, III, ... on one valve alternate with costellae II, IV, ... on the other; hence spine-rows 1, 3, ... interdigitate with spine-rows 2, 4, ... In each row there is one fully-grown 'open' spine (*a*); spines of the next set (*b*), which ultimately supersede them, are at various stages of growth (9*b* and 8*b* are most advanced, 5*b* and 4*b* least; 1*b* has not yet appeared).

The spacing between successive spines in a single row was also kept remarkably constant during ontogeny. This is particularly striking if a row on the anterior sector of the
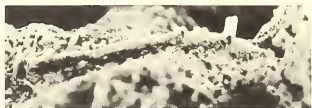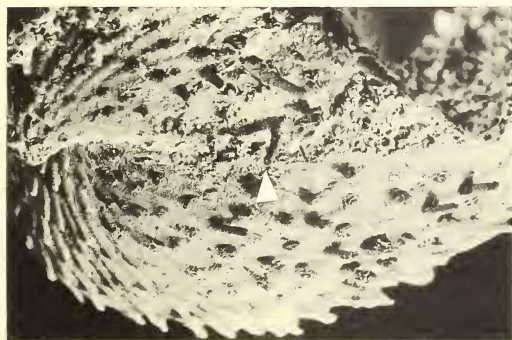
shell is compared with one of the much shorter rows on the postero-lateral sectors. The total number of spines projecting from a long row is much greater than from a short row, although both of course represent the same span of time. Yet the spacing between successive spine-bases is approximately the same (about 1·2–1·5 mm.). This implies that a new spine began to be formed at the valve-edge whenever the preceding spine had become distant from the edge by that amount, regardless of the length of time that had elapsed since the preceding spine was formed.

Comparison with spines in other shells. The related genus *Acanthorhynchia* has spines which are closely similar to those of *Acanthothiris*, except that they are on a smaller scale. Thus, where only the stumps of the spines are preserved, they form a similar but much finer pattern on the valve-surface (Pl. 87, fig. 2; compare Pl. 84, fig. 1, at same magnification). The spines themselves are very similar in appearance, but are only about 0·1 mm. in diameter near the base, though they reach over 4 mm. in length (Pl. 87, fig. 1; compare Pl. 85, fig. 2, at same magnification).

No other rhynchonelloid has comparable spines. The living species *Tegulorhynchia döderleini* (Davidson) has radial rows of very short projections, scarcely deserving the name of spines, each of which is a short incomplete tube with a slit or seam on the side nearest the valve-edge (Leidhold 1922, Taf. XIII). In this they resemble the earliest stage in the formation of a true tubular spine; but the budded-off portion of the valve-edge evidently fails to fuse into a complete isolated ring. As Leidhold pointed out, such short spines have more resemblance to the short spines of some bivalve molluscs (e.g. *Pinna*) than to the tubular spines of fossil brachiopods.

Hölder (1958) has likewise emphasized the fundamental difference between such molluscan spines and the spines of *Acanthothiris*. Nevertheless, at least one mollusc shows a moderately close, though imperfect, analogy. This is the oyster *Crassostrea echinata* (Quoy and Gaimard), which in the juvenile stage develops moderately long quasi-tubular spines. They are not truly tubular, for they invariably have a narrow slit or seam on the side nearest the valve-edge (Pl. 87, figs. 6, 8); but they may reach a length of 5 mm. at an external diameter of about 0·7 mm. They are formed by the development of an upturned 'collar' of valve-edge (Pl. 87, figs. 1, 2), which fails to fuse into a complete ring; but the further addition of incomplete rings of shell-material builds up a cylinder which, from the side furthest from the valve-edge, appears to be a complete tube (Pl. 87, figs. 5, 7). The spines project almost perpendicularly from the surface of the free (uncemented) right valve of the oyster. They are not arranged in regular radial rows, but generally occur in roughly concentric sets. Each set consists of spines which, at their time of formation, were spaced at fairly regular intervals around the edge of the valve. The set nearest the valve-edge has open apertures to the interior; earlier sets have been blocked off at the base (Pl. 87, figs. 4, 6, 8).

Rather similar spines seem to have developed in one orthoid brachiopod, *Spinorthis geniculata* Wright (1964), of Upper Ordovician age. These spines are arranged in radial rows and concentric sets, and project almost perpendicularly from the valve-surfaces. They are short, and appear to be incomplete tubes. Spines with a greater similarity to those of *Acanthothiris* have been found in an atrypoid brachiopod, *Atrypa* cf. *aspera*, of Middle Devonian age (Jux 1962). They are arranged in radial rows, and seem to have been long and tapering; it is not clear whether they were true or incomplete tubes.

Apart from such sporadic occurrences, the only genuine structural analogues to the spines of *Acanthothiris* are the spines of productoids and chonetoids. These are truly tubular spines, and were apparently formed in an identical manner, by the 'budding-off' of small portions of the valve-edge. The spines of some spiriferoids, which may be 'double-barrelled' and bear hooks or barbs, do not seem to be comparable.

FUNCTIONAL ANALYSIS

Rejected interpretations. Many functional interpretations have been suggested for spines in general, or for the spines of brachiopods in particular. Most of them, however, are clearly inapplicable to the spines of *Acanthothiris*. These are so narrow in bore, and would have been even narrower when lined with an inner tube of mantle-tissue, that it is inconceivable that they could have acted as channels for the water-currents flowing through the mantle-cavity. For the same reason, and since few of them were open at any given growth-stage, it is inconceivable that they could have increased significantly the area of mantle-tissue available for gaseous exchange. Moreover, as Hölder (1958) has pointed out, *Acanthothiris* is generally found in calcareous sediments, which are unlikely to have been deposited in poorly aerated conditions. The spines are fragile (at least in the fossil state: they would have been less so when the organic component of the shell-material was still present); and once they were broken they could not be repaired (unless they were still 'open'). It is therefore difficult to believe that they performed any porcupine-like function of protection against large predators. On the other hand, it is perhaps possible that they might have served to camouflage the shell, by breaking up its otherwise sharp and distinctive outline. This fails to account, however, for most of the detailed characteristics of the spines. Finally, whatever the natural orientation of the shell, most of it must have been above the level of the substratum, in order to provide the apertures with clear access to food- and oxygen-bearing water. Hence only a few of the spines (probably the earliest, in the umbonal region) could ever have served to anchor the shell in a soft substratum (cf. text-fig. 3в). Unlike the rhizoid spines of productoids (Muir-Wood and Cooper 1960), the spines of *Acanthothiris* have never been found cemented to substratal material.

Spines as a sensory mechanism. A more promising interpretation can be derived from knowledge of the sensory mechanisms of living articulate brachiopods. Although the exact nature of the sensory receptors is at present unknown, they are apparently confined to the extreme edge of the mantle. The mantle-edge is highly sensitive to touch, light, and some chemical stimuli, and is richly supplied with nerve-endings. (If setae are present, they too are sensitive, but only to tactile stimuli.) A simple reflex nerve circuit from the mantle-edge causes the shell to be snapped shut in response to stimuli (Rudwick

EXPLANATION OF PLATE 85

Figs. 1–5. *Acanthothiris spinosa* (Schlotheim); Inferior Oolite (Middle Jurassic); Bath, England. 1. Later spines on dorsal valve of SM J57756, ×6, showing radial orientation and gently tapering form. 2. Umbonal region and right postero-lateral sectors of SM J57759, ×9, showing structure of stumps of spines, and their early origin. 3. Spines on left lateral sector of dorsal valve of MCZ 5794*a*, ×6, showing radial orientation. 4. The same, on SM J57757, ×6. 5. Later spines on anterior sector of (broken) dorsal valve of MCZ 5794*b*, ×6, showing gently tapering form.
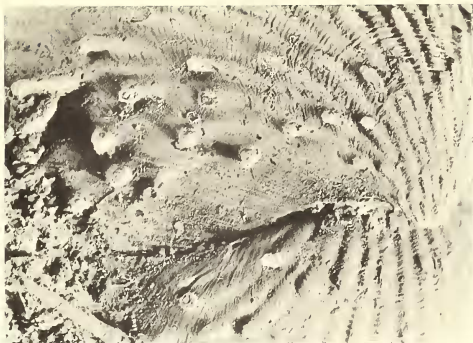
1961). Hence any modification of the form of the mantle-edges can be considered as a possible modification of this protective system. For example, sharply zigzagged valve-edges would have reduced the distance between the sensitive mantle-edges without any corresponding reduction in the area of the apertures (Rudwick 1964*a*). This would have improved the quality of protection at the apertures, but would not have given the brachiopod any *earlier* warning of the approach of potentially harmful agents. Early warning could only be provided by extending the sensitive mantle-edges, or parts of them, outwards away from the rest of the shell. This would have been precisely the effect of the spines of *Acanthothiris*. Each of the 'open' spines would have carried at its tip a small piece of the sensitive mantle-edge tissue (and possibly, but not necessarily, one or more setae). Assuming only that at least one of the many peripheral nerve-fibres extended along each spine, the tip would have formed a highly sensitive 'outpost' of the brachiopod's protective system, giving early warning of the approach of harmful agents and enabling the shell to be snapped shut well in advance.

The paradigm, or optimal specification for this function (Rudwick 1964*b*), is fairly easy to determine. Ideally the tips of the spines might be situated very far from the shell, but in reality the length of the spines would presumably be limited by the supply of material available for their construction and by the strength of the material itself. They would need to be as slender as possible, consistent with strength, since they would otherwise tend to obstruct the free flow of the water-currents in and out of the mantle-cavity. A cylindrical form is of course the most effective shape by which to combine strength with economy. Their sensitive tips would be disposed most effectively if they were situated at uniform intervals all round the approaches to the apertures. With the continuing growth of the shell, the tips of these 'active' spines would inevitably be shifted further and further from the apertures, and would gradually become less effective; and they would need to be replaced by new spines, projecting from the valve-edges in their new position.

The observed structure and arrangement of the spines of *Acanthothiris* fit this speci-fication very well. If the tips of the 'open' spines are identified as the points of chief functional importance, much that is otherwise obscure about the spines becomes intelligible. This interpretation explains the radial orientation and regular spacing of the spines in each set; the time-sequence of growth and blockage that marks each row; and their slender cylindrical form. It implies that only the most recently formed sets of spines were fully functional at any given growth-stage; and that all the earlier spines had been superseded and had become functionally redundant through the inevitable shift in their relative position (text-fig. 3A, B).

The range of sensitivity around each spine-tip would depend on the sensitivity of the mantle-edge tissue. This in turn would probably depend on properties at the cellular level, which would be unlikely to change in proportion to the growth of the whole organ-ism. There would therefore be certain optimal distances for the spacing of adjacent spine-tips, both between spines in adjacent rows, and between successive spines in the same row; and these optimal values would remain relatively constant during ontogeny. Although the validity of this aspect of the paradigm cannot be demonstrated conclusively, it is at least probable, and it would explain the remarkable constancy in the spacing of the spines.

This interpretation is compatible with another, slightly different, concept of protection.

The peripheral spines, by their orientation and slight curvature towards the oppo-
site valve, would have interdigitated when the shell was closed. When the valves gaped
apart through a small angle (as they do in living brachiopods), and water-currents were
being pumped by the lophophore through the mantle-cavity, the same spines would
therefore have straddled the apertures with a protective grille (text-fig. 2). No 'particle'
(e.g. a swimming animal or piece of floating debris) larger than the spaces between
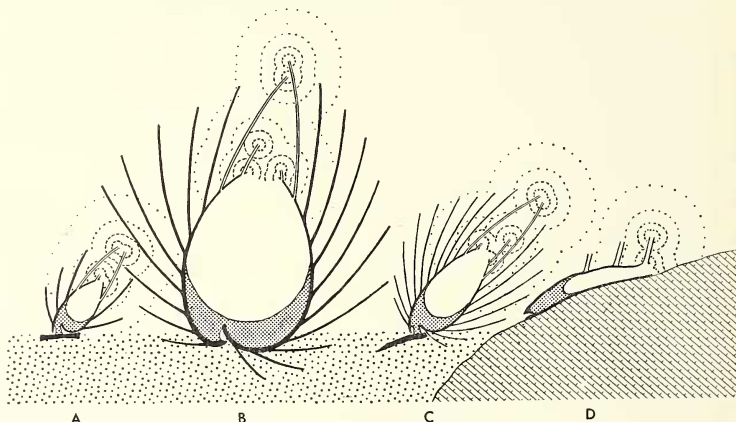
TEXT-FIG. 3. Reconstructions of *Acanthothiris* (A, B) and *Acanthorhynchia* (C), with analogous section
of *Crassostrea* (D), showing functional interpretation of spines as sensory 'antennae'. Note peripheral
'open' spines and earlier 'blocked' spines. 'Contours' of chemo-sensitivity (radii arbitrary) shown
around open spine-tips and mantle-edges; for tactile sensitivity all the spines would be operative, and
the protection would surround the whole shell. Reconstructions based on conservative estimates of
original length of spines. 'Body' of animals close-stippled; lophophore, gills, &c., omitted. About
× 1·5.

A, young *Acanthothiris*, with pedicle attached to shell fragment. B, adult *Acanthothiris*, with pedicle
atrophied, resting loosely on unconsolidated substratum. C, *Acanthorhynchia*, with similar but more
slender spines, and smaller shell. D, young *Crassostrea echinata*, with broad tubular spines on upper
(right) valve, left valve cemented to rock surface.

EXPLANATION OF PLATE 86

Figs. 1–7. *Acanthothiris spinosa* (Schlotheim); Inferior Oolite (Middle Jurassic); Bath, England.
    1. Rows of spines on right antero-lateral sectors of SM J57757, × 6, showing slight curvature
    towards commissure. 2. Interior of right antero-lateral sector of dorsal valve of SM J57753, × 6,
    showing broad peripheral zone of unblocked spine-apertures. 3. Oblique view of same valve-edge,
    × 6, showing connexion between two marginal apertures and their respective spines. 4. Very young
    spines on peripheral part of left antero-lateral sector of dorsal valve of SM J57756, × 6. 5. Close-up
    of spines on anterior sector of dorsal valve of SM J57757, × 18, showing shell-structure and growth-
    lines (*not* whitened). 6. Interior of left antero-lateral sector of MCZ 5794b, × 6, showing narrow
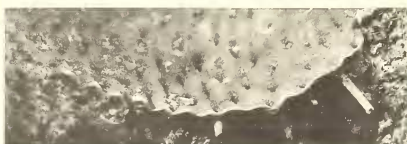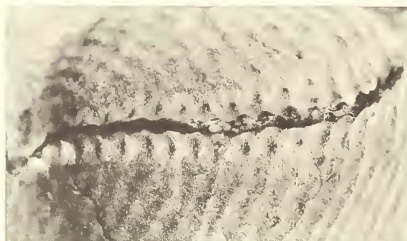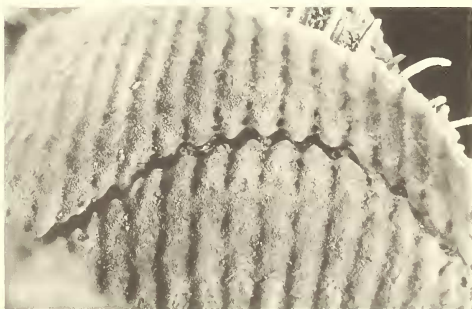   peripheral zone of unblocked spine-apertures. 7. The same, anterior sectors, × 6.